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A Study of Wilt Resistance in Flax

By H. D. Barker
Division of Plant Pathology and Botany
In Co-operation With
Division of Agronomy and Farm Management

UNIVERSITY FARM, ST. PAUL

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A STUDY OF WILT RESISTANCE IN FLAX

By H. D. Barker[1]

INTRODUCTION

Statistics of the United States Department of Agriculture[2] show that the production of oil flax in this country has steadily decreased. The average annual production from 1902 to 1911 was 23,749,000 bushels, and from 1912 to 1921 it was 13,668,000 bushels. This does not seem to be due to a lessened demand for linseed in this country. From 1902 to 1911 the average annual import was 2,375,700 bushels, with an annual average export of 2,264,400 bushels. The average export about equals the average import for the ten-year period because in the latter part of the period we changed from a flaxseed exporting nation to an importing one. From 1912 to 1920 the average annual import amounted to 12,637,800 bushels with an average export of 44,700 bushels. In Minnesota the average annual production from 1902 to 1911 was 4,911,600 bushels, while from 1912 to 1921 it was only 2,943,500. There was a similar diminution in other states. The center of flax production has steadily moved westward to new lands. For that reason flax has frequently been called a new-land crop. Notwithstanding the fact that it thrives better on new land than certain other crops and is less damaged by weeds, it may grow equally well on old lands if they are properly prepared and if wilt can be controlled.

Flax wilt is a very important factor in this decrease in flax production and in the westward migration of the crop. It is well known that when flax is grown for more than one year on the same soil the yields decrease. Because of this such soil has been termed "flax sick" soil. The disease has in reality become a limiting factor in the production of flax in certain states.

DISTRIBUTION OF THE DISEASE

Flax wilt is probably prevalent throughout the flax growing regions of the world, particularly in the seed flax areas where it is one of the most destructive diseases. Finch and Baker (11) state, "Because of the liability to disease when grown continuously on the same land, flax is grown almost universally on new lands in the United States, Canada, and Argentina. Newly turned prairie sod is very commonly

[1] The writer wishes to acknowledge his indebtedness to Dr. E. C. Stakman of the section of plant pathology and to Dr. H. K. Hayes of the section of plant breeding, for their aid in defining the problems at the outset and for their supervision and kindly criticism of the work.

[2] United States Department of Agriculture Yearbooks.

sown to flax before a crop of wheat is put on the land. In the Russian fiber crop region newly cleared scrub lands are often employed and in the Netherlands the newly reclaimed 'ploder lands.' "

SYMPTOMS OF THE DISEASE

The symptoms of flax wilt have been described in considerable detail by Bolley (1, 2). However, it may not be out of place to describe some of the more outstanding symptoms, particularly as they occur in Minnesota.

Plants may be attacked at any stage of development. In the early seedling stage they may simply "damp-off." The roots may be completely rotted. Somewhat later, when a certain amount of lignified tissue has developed in the plants, they no longer fall over but any one of many things may happen when they are attacked by the wilt fungus. If the attack is rapid and severe, complete wilting and death result. In other cases the plant may appear to be only slightly stunted or to be very unthrifty and some of the leaves may turn yellow and fall off; or the top of the plant may die and new, apparently healthy, vigorous branches may grow. Frequently only one side of the plant is affected. This is particularly true of older plants. The normal green and the dead, browned areas extend side by side up the plant and are sharply delimited from each other. In partly wilted plants the crown of the plant and the main root or underground portion of the stem may be enlarged considerably. Very late infection may find expression only in premature ripening and browning of the plants. In most of the Fusarium wilt diseases the vascular tissue of the stem near the crown of the plant is blackened or browned. This symptom often appears in flax plants that are seriously affected with the disease, altho it is by no means a universal symptom.

HISTORICAL REVIEW

The importance of disease resistance in plants, and discussions of the more important literature on the development of disease resistant varieties, have been so well and so thoroly summarized in many recent papers that only those are cited in this paper which deal particularly with flax wilt and the problems relating to the development of wilt-resistant varieties in general.

Little is known definitely regarding the early history of flax wilt. Neither is the origin of our cultivated varieties of flax well known. According to Hayes and Garber (13 p. 153) flax was grown by the Lake Dwellers of Switzerland as early as 4000 B.C. Vague descriptions in the older literature indicate that wilt may have been a serious factor

in flax production for a long time. Pliny (19 p. 131), in discussing flax, remarks, "It has the property of scorching[3] the ground where it is grown and of deteriorating the quality of the very soil itself."

While the disease has undoubtedly existed in European countries for a long time, the early history of flax diseases is difficult to determine because the descriptions in the older literature are meager. The nature of the wilt disease was not known and hence different names were applied to it. It was for a long time regarded as a soil trouble. It was thought that flax extracted large amounts of food from the land, or that injurious substances were developed by it.

Broekema (9), in 1893, was among the first to separate this disease from others which had gone under the loose term "Brand." He noted the destructiveness of the disease and suspected that it was caused by a parasite. He observed resistant plants that remained healthy and vigorous in the midst of plants that had succumbed to the disease. He definitely raised the question as to whether this quality might be hereditary, and selected seeds from plants which showed no external manifestations of the disease and planted these beside seed of non-selected sorts. He decided that the plants from the selected seed developed better than the others and were much less affected with the disease; also that the susceptibility of the seedlings from such plants diminishes when compared with that of plants from non-selected seed. One of the explanations he suggested was that the descendants of resistant plants had by nature a force for greater growth and consequently greater vitality and resistance to the "Vlasbrand."[4]

Nypels (16), in 1897, called attention to the seriousness of a disease which was widespread throughout the Pays-Bas and Flanders, where it was called "Vlasbrand," and which he calls "La brulure du lin." He calls particular attention to its destructiveness and points out that on badly diseased soil it may destroy the crop. He gives Broekema credit for separating the disease from a great many others which had been termed "Vlasbrand." He also discusses a disease which he terms "l'etetement du lin" (l. c. pp. 220-21), describing the symptoms and the possible causes. From his descriptions and figures (l. c., figs. 5 and 6, p. 226), it seems quite possible that he was dealing with flax wilt.

Bolley (1, 2) demonstrated that the cause of flax wilt was *Fusarium lini* Bolley. Seed treatment and crop rotation were shown by him to be beneficial in the control of the disease. As Broekema had done earlier, Bolley (3, 5, 6) also observed that in infested fields a few

[3] The following footnote of the translator is made: Virgil says, Georg. i 77, "Urit enim lini campum seges" – but in the sense, as Fee remarks, of exhausting, not scorching the soil.

[4] Portions of the original paper, published in the Dutch language, were translated by J. B. Osborn, a graduate student in Biochemistry.

plants did not succumb to the attacks of the disease when most of the plants were killed, and that a few scraggly plants survived the first year when varieties were grown on sick soil. These were selected and the progeny was somewhat resistant the following year. After several years of selection, sorts were produced which yielded well on sick soil. He states (8, p. 3), "How we obtained resistant flax plants is, in a large part, explained in previous portions of this bulletin, but no scientist has yet been able to explain just why the plants become resisant when exposed generation after generation to the action of the disease. Our experiments leave no question but that when the disease character is held constant so as to act steadily upon the roots and crop that generation after generation accumulates more resistance until there comes a time when the disease in the ground has no longer any ability to cut down the yield."

In general Bolley concluded that two or three years' selection under disease conditions were necessary in order to isolate a resistant variety. Both individual and mass selection methods were used. At the Minnesota station, Stakman et al. (20) confirmed Bolley's remarkable results.

Tisdale (21, 22) has made very important contributions to the literature on the nature and inheritance of wilt resistance in flax. He found that resistance is only relative, owing to the profound modifying effects of environmental factors, especially temperature. At high temperatures the most resistant varieties may wilt severely, while at low temperatures susceptible varieties may escape infection. The fungus enters either susceptible or resistant plants through the stomata of the seedlings, the root hairs, and perhaps through wounds. In resistant plants, the fungus, upon entering, stimulates cork wall formation of cells adjacent to those attacked. This perhaps prevents further invasion. From experiments on hybridization, Tisdale found a marked difference in the individuality of plants of the same strain with respect to resistance in the progeny. Part of the lack of uniformity resulting from crosses between resistant and susceptible plants could be explained by varying environmental conditions. He concluded that wilt resistance is an inheritable character which is apparently determined by multiple factors.

Orton (17) developed varieties of cotton resistant to wilt, Jones and Gilman (14) varieties of cabbage resistant to yellows, and Essary (10) varieties of tomatoes resistant to wilt. Other investigators secured similar results in developing selections of plants resistant to various Fusarium wilt diseases.

Jones and Gilman (14) and Jones, Walker, and Tisdale (15) succeeded in securing varieties of cabbage resistant to *Fusarium conglutinans* Wollenw. They found that there are occasionally healthy plants even in the worst diseased fields. Selection of these gave rise to highly resistant strains. Repeated selection seemed to result in increased resistance. The degree of resistance was found to be relative. Environmental factors, especially soil temperature, influenced the development of the disease and also the disease resistance of the host. It is concluded (14 p. 34) that "It seems probable that in case the resistant strains are propagated through successive generations without repeated selection, they will tend to lose to some extent the disease resistant character."

One of the very striking peculiarities discovered by Bolley was that resistant varieties lose their resistance after they have been grown for a few years on disease-free soil. This is summarized by Hayes and Garber (13 p. 158) as follows: "Whether this behavior is a gradual decrease in resistance of the host which is roughly proportional to the length of time which the resistant variety has grown on wilt-free soil or a more or less sudden change which appears after two or three years is as yet unknown."

DEFINITION OF PROBLEM

The work of Bolley (3, 5) in securing wilt-resistant flax and of others (10, 14, 18, 20) in securing varieties of crop plants resistant to Fusarium wilts, has shown that these serious diseases can be controlled by selecting wilt-resistant types. The results in many of these cases have been similar, regardless of the differences in the crops concerned, and have indicated that resistance to wilt may be different from other types of resistance. There has been much theorizing as to the nature of this resistance and the difficulties of explaining the peculiar and striking results on the basis of the pure-line theory. It is apparent that the problem is of immense practical and fundamental importance.

In view of these facts the objects of the present investigation, which was conducted as a co-operative project between the section of plant pathology and the section of plant breeding, were:

1. To determine whether the results in selecting wilt-resistant varieties of flax could best be explained by the pure-line theory.
2. To study the effects of continued selection for wilt resistance in flax.
3. To determine whether resistance could be built up in any commercial variety of flax, or if it is a peculiar quality possessed only by certain varieties or groups of varieties.

4. To determine whether resistant varieties lose their resistance when grown on clean soil.
5. To study the relation of time of planting to the control of flax wilt.
6. To study the comparative resistance and yielding ability of the most promising selections of wilt-resistant varieties obtained at this station by previous selection.

SOURCE OF MATERIAL

The field studies were made on soil that had been continuously cropped to flax since 1914, when it was inoculated with pure cultures of *Fusarium lini.* This soil proved to be heavily infested with the pathogene in all the tests conducted on it. Several individual and bulk selections made by Stakman et al. (20) were available for further study. A short history of each of the important selections is given in Table I.

INDIVIDUAL PLANT SELECTION STUDIES

METHODS USED IN MAKING SELECTIONS

Individual plants were selected from a large number of resistant plants from the various selections, as indicated in Table I. These were labeled "R" (resistant) indicating that the plants selected were the most vigorous that could be found in several thousand of that particular selection and that such plants showed no visible symptoms of infection with *Fusarium lini.* The label "PR" indicated that the plant selected was "partly resistant"; that is, had recovered sufficiently to produce some seed. In such cases the mainfestation of wilt was variable. Frequently the central stalk had wilted and died back; or, less frequently, lateral branches were similarly affected; or in many cases one side of the stalk had been killed while the other side was sufficiently healthy to mature some seed. The selections were made when the first bolls had begun to mature.

TABLE I

INDIVIDUAL PLANT SELECTIONS MADE IN 1919

Selection	Remarks	History of parent selection
M25-1R.........	Normal plant	Primost, Minn. No. 25, (C. I. No. 47). Unselected for wilt resistance. The average percentage of wilt in this variety on the plant pathology plots from which the individual plant selections were made was 95.
M25-2R.........	Possibly slight wilt Plant slightly yellow	
M25-3R.........	Normal plant	
M25-4R.........	Normal plant	
M25-5R.........	Very exceptional vigor	
M25-6R.........	Normal plant	
M25-7PR to 13PR	Partly wilted	
25-7-1R to 25R.........	Normal plants	*Selection Plot IV 25-7, a wilt-resistant selection produced by bulk selection in 1914 and individual plant selection in 1915 from Primost, Minn. 25. The selection Plot IV-25-7 was subsequently named Chippewa, Minn. No. 181 (C. I. No. 178). Average percentage of wilt in 1919 was 4.
25-7-26PR to 31PR.......	Partly wilted	
25-7-32R to 56R.........	Normal plants	
175-1-1R to 25R.........	Normal plants	*Selection Plot III 175-1, a wilt-resistant selection produced by bulk selection in 1915 and individual plant selection in 1916, from Blue Dutch, Minn. No. 175. This selection was subsequently named Winona, Minn. No. 182 (C. I. No. 179). Average percentage of wilt in 1919 was 4.
175-1-26PR to 29PR.......	Partly wilted	
175-1-30R to 54R.........	Normal plants	
91-1-1R to 25R...	Normal plants	*Plot II 91-1, a wilt-resistant selection produced by bulk selection in 1914 and 1915 and by individual plant selection in 1916, from Minn. No. 91. Average percentage of wilt in 1919 was 37.
91-1-26PR to 30PR.......	Partly wilted	
74-1-1R to 25R...	Normal plants	Selection Plot IV 74-1, a wilt-resistant selection produced by bulk selection in 1914 and individual plant selection in 1915, from Minn. No. 74. Average percentage of wilt in 1919 was 22.
74-1-26PR to 30PR.......	Partly wilted	
II-09-15-1-1R to 10R........	Normal plants	Selection II-09-15-1, Minn. 163, a selection for high yielding quality made from a 1909 cross between "Cantania" and "Improved." The selection II-09-15-1 had shown a certain degree of resistance in the field but was not selected for wilt resistance. Average percentage of wilt in 1919 was 91.
II-09-15-1-11PR to 25PR.......	Partly wilted	

* The original selections were made by the section of plant pathology.

METHODS OF SELFING SELECTIONS

Selfing was accomplished by growing the selections in the greenhouse during the winter, each plant in a separate booth formed by double walls of cheese-cloth. In this way many seeds were produced from a single plant. In a few cases selfing was done in the field by placing a cigarette tube over each flower. However, for the studies here recorded selfing was done in the greenhouse, part of the seed being saved each year for selfing in the greenhouse the following year. The rest was planted in individual rows on sick soil. A list of the parent types with a short history of each is given in Table I. This also includes outstanding features of each selection.

RESULTS OBTAINED FROM INDIVIDUAL SELECTIONS

A large number of individual plant studies were made in order to determine whether the peculiar results obtained in selecting varieties of plants resistant to wilt could be explained by the pure-line theory; to test the effect of continued selection upon the development of wilt resistance; and to determine whether resistance could be built up in any commercial selection of flax if it was continuously associated with the disease. The question naturally arose as to whether the results in obtaining wilt-resistant strains of flax could not best be explained by the pure-line theory. Other questions were: By what means does flax become resistant? What is the explanation for the widespread opinion that resistance is gradually "built up" by the association of the plant and the parasite? Why is resistance lost by the long-time removal of the plant from sick soil? Why could resistance be built up only to a certain point regardless of the method employed? Would it be possible to obtain by continuous individual plant selection and careful self-pollination, varieties that would be immune from wilt? These questions could not be answered on the basis of definite experimental proof at hand, hence it was decided to make a large number of individual plant selections and self these for several generations, if necessary, in order to be certain that homozygous selections were secured, to see what light they could throw on the problem. Accordingly, in the summer of 1919 about five hundred individual plant selections were made from the selections grown on sick soil on the plant pathology plots.

Plant selections were made as already described. A summary of these selections with a brief history of the parent type is given in Table I. These were grown in sterilized soil in the greenhouse in the winter of 1919-20. The results of the tests after one generation of selfing are given in Tables II and III.

TABLE II

REACTION OF INDIVIDUAL PLANT SELECTIONS FROM WILT-FREE PLANTS (R), IN 1919, SELFED IN GREENHOUSE DURING THE WINTER OF 1919-20, AND PLANTED ON SICK SOIL IN 1920

Selection	No. of plants	Killed by wilt		Partially wilted		Total per cent of wilt
		No.	Per cent	No.	Per cent	
M25-2R	24	3	12.5	8	33.3	45.8
M25-3R	23	4	17.4	16	69.6	87.0
M25-4R	13	1	7.7	7	54.0	61.7
M25-5R	76	7	9.2	32	42.2	51.4
M25-6R	50	21	42.0	11	22.0	64.0
Total	186	36	88.8	74	221.1	309.9
Average	37.2	7.2	17.8	15.8	44.2	62.0
25-7-2R	15	1	6.7	1	6.7	13.4
25-7-3R	10	4	40.0	2	20.0	60.0
25-7-[illegible]R	6	1	16.7	2	32.3	50.0
25-7-6R	40	8	20.0	17	42.5	62.5
25-7-7R	10	1	10.0	1	10.0	20.0
25-7-8R	15	0	0.0	4	26.8	26.8
25-7-9R	3	0	0.0	2	66.7	66.7
25-7-10R	63	13	20.3	11	17.5	37.8
25-7-11R	80	19	24.8	20	25.0	48.8
25-7-12R	29	4	13.8	4	13.8	27.6
25-7-13R	9	0	0.0	1	11.1	11.1
25-7-14R	1	0	0.0	0	0.0	0.0
25-7-16R	75	11	14.7	23	30.3	45.0
25-7-17R	80	15	18.7	24	30.0	48.7
25-7-18R	40	11	27.5	7	17.5	45.0
25-7-19R	139	39	28.1	28	20.1	48.2
25-7-20R	104	21	20.1	25	24.0	44.1
25-7-21R	107	22	20.6	36	33.6	54.2
25-7-22R	7	1	14.3	0	0.0	14.3
25-7-25R	5	0	0.0	1	20.0	20.0
25-7-32R	16	1	6.2	9	56.1	62.3
25-7-33R	71	6	8.5	32	45.1	53.6
25-7-34R	2	0	0.0	2	100.0	100.0
25-7-35R	79	6	7.6	17	21.5	29.1
25-7-36R	17	0	0.0	5	29.4	29.4
25-7-37R	17	2	11.7	6	35.3	47.0
25-7-38R	38	5	13.2	13	34.1	47.3
25-7-39R	69	22	31.8	16	23.2	55.0
25-7-40R	3	0	0.0	3	100.0	100.0
25-7-41R	11	1	9.1	5	45.5	54.6
25-7-42R	25	2	8.0	13	52.0	60.0
25-7-43R	2	0	0.0	1	50.0	50.0
25-7-45R	100	13	13.0	26	26.0	39.0
25-7-47R	118	15	12.5	35	29.6	42.1
25-7-48R	80	19	23.8	26	32.6	56.4
25-7-49R	55	3	5.5	20	36.3	41.8
25-7-50R	69	8	11.6	21	30.4	42.0
25-7-51R	113	11	9.7	30	26.5	36.2
25-7-52R	92	5	5.5	37	40.1	45.6
25-7-53R	9	0	0.0	2	22.2	22.2
25-7-54R	58	17	29.3	20	34.5	63.8
25-7-55R	12	1	8.4	9	75.0	83.4
25-7-56R	26	3	11.6	6	23.1	34.7
Total	1920	311	523.3	[illegible]63	1416.4	1939.7
Average	37	7.2[illegible]	13.[illegible]	13.1	32.9	4[illegible].1

TABLE II—*Continued*

Selection	No. of plants	Killed by wilt		Partially wilted		Total per cent of wilt
		No.	Per cent	No.	Per cent	
175-1-1R	23	0	0.0	6	26.1	26.1
175-1-2R	45	7	15.6	16	35.6	51.2
175-1-3R	42	6	14.3	12	28.3	42.6
175-1-5R	123	20	16.3	27	22.0	38.3
175-1-7R	48	3	6.2	5	10.4	16.6
175-1-8R	30	5	16.7	7	23.2	39.9
175-1-9R	29	6	20.7	8	27.6	48.3
175-1-11R	49	9	18.8	9	18.8	37.6
175-1-12R	68	13	19.2	10	14.7	33.9
175-1-13R	12	1	8.3	5	41.7	50.0
175-1-14R	55	8	14.5	19	34.6	49.1
175-1-17R	35	4	11.4	9	25.8	37.2
175-1-19R	1	1	100.0	0	0.0	100.0
175-1-20R	12	0	0.0	4	33.4	33.4
175-1-21R	4	2	50.0	0	0.0	50.0
175-1-23R	1	0	0.0	0	0.0	0.0
175-1-24R	60	6	10.0	5	8.3	18.3
175-1-30R	33	2	6.0	5	15.2	21.2
175-1-32R	41	6	14.6	4	9.8	24.4
175-1-33R	40	1	2.5	4	10.0	12.5
175-1-35R	38	8	20.0	1	2.6	23.6
175-1-36R	29	0	0.0	5	17.4	17.4
175-1-37R	78	2	3.8	10	12.8	16.6
175-1-38R	52	1	1.9	2	3.8	5.7
175-1-40R	4	0	0.0	1	25.0	25.0
175-1-42R	6	0	0.0	2	33.3	33.3
175-1-43R	63	6	9.5	4	6.4	15.9
175-1-46R	58	7	12.1	4	6.9	19.0
175-1-47R	9	0	0.0	0	0.0	0.0
175-1-48R	10	0	0.0	0	0.0	0.0
175-1-49R	29	4	13.8	5	17.3	31.1
175-1-50R	30	2	6.7	3	10.0	16.7
175-1-52R	62	4	6.5	9	14.5	21.0
175-1-53R	29	3	10.3	2	6.9	17.2
175-1-54R	36	11	30.6	2	5.5	36.1
Total	1284	148	460.3	205	547.9	1012.2
Average	36.8	4.2	13.2	5.9	15.7	29.0
91-1-3R	62	4	6.5	29	46.7	53.2
91-1-4R	117	24	20.6	41	35.0	55.6
91-1-5R	97	21	21.6	33	34.0	55.6
91-1-7R	39	4	10.3	14	35.9	46.2
91-1-8R	119	14	11.8	62	52.1	63.9
91-1-9R	18	2	11.1	5	27.8	38.9
91-1-10R	34	1	2.9	9	26.5	29.4
91-1-11R	69	17	24.6	44	63.7	88.3
91-1-12R	38	2	5.3	6	15.7	21.0
91-1-13R	49	5	10.0	13	26.7	36.7
91-1-14R	46	4	9.6	13	28.2	36.8
91-1-15R	142	13	9.1	38	26.8	35.9
91-1-16R	91	13	14.3	48	52.7	67.0
91-1-17R	143	14	9.8	57	40.0	49.8
91-1-19R	50	5	10.0	31	62.0	72.0
91-1-20R	113	20	17.7	82	72.6	90.3
91-1-22R	24	3	13.0	11	47.9	60.9
91-1-23R	28	0	0.0	13	46.4	46.4
91-1-24R	23	0	0.0	10	43.5	43.5
Total	1302	166	208.2	559	784.2	991.4
Average	[illegible]	8.8	11.0	28.4	[illegible]	[illegible]

TABLE II—*Concluded*

Selection	No. of plants	Killed by wilt		Partially wilted		Total per cent of wilt
		No.	Per cent	No.	Per cent	
74-1-3R	22	3	13.7	10	45.5	59.2
74-1-4R	101	4	4.0	30	30.0	34.0
74-1-[illegible]R	138	9	6.5	41	29.8	36.3
74-1-8R	137	4	3.0	48	35.0	38.0
74-1-9R	63	1	1.6	14	22.2	23.8
74-1-10R	64	2	3.1	15	23.5	26.6
74-1-11R	48	4	8.3	17	35.4	43.7
74-1-14R	39	7	18.0	13	33.4	51.4
74-1-15R	72	3	4.1	13	18.1	22.2
74-1-[illegible]R	45	2	4.4	16	35.6	40.0
74-1-17R	39	3	7.7	10	25.6	33.3
74-1-19R	94	4	4.2	22	23.4	27.6
74-1-21R	141	20	14.2	62	44.0	58.2
74-1-22R	32	2	6.2	4	12.5	18.7
74-1-23R	27	2	7.4	1	3.7	11.1
74-1-24R	40	4	10.0	12	30.0	40.0
74-1-25R	22	1	4.5	8	36.5	41.0
Total	1124	75	120.9	336	484.2	605.1
Average	66.2	4.4	7.1	19.8	28.5	35.6
II-09-15-1-3R	118	38	32.3	25	21.2	53.5
II-09-15-1-5R	27	8	29.6	6	22.4	52.0
II-09-15-1-6R	98	25	25.5	45	45.9	71.4
II-09-15-1-7R	82	21	25.6	21	25.6	51.2
II-09-15-1-8R	109	29	26.6	18	16.5	43.1
II-09-15-1-10R	3	2	66.7	0	0.0	66.7
Total	437	123	206.3	109	131.6	337.9
Average	73	20.5	34.3	18.2	21.9	56.2

TABLE III

REACTION OF INDIVIDUAL PLANT SELECTIONS FROM PARTIALLY WILTED PLANTS (PR), IN 1919, SELFED IN GREENHOUSE DURING THE WINTER OF 1919-20, AND PLANTED ON SICK SOIL IN 1920

Selection	No. of plants	Killed by wilt		Partially wilted		Total per cent of wilt
		No.	Per cent	No.	Per cent	
M25–7PR	83	10	12.0	31	37.4	49.4
M25–8PR	56	2	3.6	28	50.0	53.6
M25–9PR	81	25	30.9	42	51.8	82.7
M25–10PR	52	1	1.9	18	34.6	36.5
M25–11PR	14	3	21.4	6	42.9	64.3
M25–12PR	100	12	12.0	27	27.0	39.0
M25–13PR	25	4	17.4	8	34.8	52.2
M25–14PR	80	15	18.7	35	43.8	62.5
M25–15PR	87	32	36.8	44	50.5	87.3
M25–16PR	15	3	20.0	8	53.4	73.4
M25–17PR	19	3	15.8	5	26.4	42.2
Total	612	110	190.5	252	452.6	643.3
Average	55.6	10	17.3	11.9	41.1	58.5
25–7–27PR	44	6	13.6	11	25.0	38.6
25–7–28PR	99	17	17.2	32	32.2	49.4
25–7–29PR	8	1	12.5	3	37.5	50.0
25–7–30PR	76	12	15.7	20	26.3	42.0
Total	227	36	59.0	66	121.0	180.0
Average	56.8	9	14.8	16.5	30.3	45.0
175–1–26PR	66	51	77.3	1	1.5	78.8
175–1–27PR	42	18	42.9	4	9.5	52.4
175–1–29PR	25	4	16.0	4	16.0	32.0
Total	133	73	136.2	9	27.0	163.2
Average	44	24.3	45.4	3.0	9.0	54.4
91–1–26PR	103	8	7.7	38	37.0	44.7
74–1–26PR	50	4	8.0	11	22.0	30.0
74–1–27PR	40	4	10.0	10	25.0	35.0
74–1–28PR	49	2	4.1	11	22.5	26.6
74–1–29PR	128	7	5.5	35	27,2	32.7
Total	267	17	27.6	67	96.7	124.3
Average	66.8	4.3	6.9	16.8	24.2	31.1
II–09–15–1–11PR	27	9	33.3	3	11.1	44.4
II–09–15–1–12PR	33	6	18.4	13	39.4	57.8
II–09–15–1–14PR	142	53	37.3	80	56.4	93.7
II–09–15–1–15PR	60	10	16.7	29	48.3	65.0
II–09–15–1–19PR	114	41	36.0	31	27.2	63.2
II–09–15–1–20PR	95	32	33.6	51	53.6	87.2
II–09–15–1–21PR	120	49	40.9	48	40.1	81.0
Total	591	200	216.2	255	276.1	492.0
Average	84.5	28.6	30.8	56.4	39.5	70.3

TABLE IV

INDIVIDUAL PLANT SELECTIONS MADE IN 1919 FROM RESISTANT PLANTS (R), SELFED FOR TWO GENERATIONS IN THE GREENHOUSE, AND PLANTED ON SICK SOIL IN 1921

Selection	No. of plants	Wilted	
		No.	Per cent
M25-4R	40	40	100.0
M25-5R	61	3	4.9
M25-6R	30	3	10.0
Total	131	46	114.9
Average	43.7	15.3	38.3
25-7-5R	6	0	0.0
25-7-6R	41	3	7.3
25-7-7R	13	0	0.0
25-7-8R	62	9	14.5
25-7-10R	23	1	4.4
25-7-11R	36	3	8.3
25-7-14R	14	1	7.2
25-7-17R	60	6	10.0
25-7-21R	15	1	6.7
25-7-25R	13	3	2.3
25-7-33R	24	2	8.3
25-7-36R	9	0	0.0
25-7-37R	28	5	17.9
25-7-38R	34	6	17.6
25-7-41R	5	0	0.0
25-7-45R	74	1	1.4
25-7-47R	31	2	6.5
25-7-48R	30	6	20.0
25-7-51R	3	2	66.7
25-7-52R	38	8	21.1
Total	559	59	220.2
Average	28	3	11.0
175-1-1R	65	1	1.5
157-1-2R	28	6	21.5
175-1-3R	45	15	33.3
175-1-5R	29	5	17.2
175-1-7R	83	6	7.2
175-1-12R	44	3	6.8
175-1-23R	79	24	30.2
175-1-25R	30	4	13.3
175-1-32R	20	4	20.0
175-1-33R	91	12	13.2
175-1-36R	13	5	38.5
175-1-37R	44	18	40.9
175-1-38R	7	2	28.6
175-1-40R	21	9	42.9
175-1-43R	49	18	36.8
175-1-46R	77	19	24.7
175-1-47R	24	11	45.8
175-1-48R	71	36	50.7
175-1-49R	96	44	45.8
175-1-50R	86	34	39.5
175-1-52R	14	6	42.9
175-1-53R	51	19	37.3
175-1-54R	34	15	44.1
Total	1101	316	682.7
Average	47.9	13.7	29.7

TABLE IV—*Continued*

Selection	No. of plants	Wilted	
		No.	Per cent
91-1-3R	36	29	80.6
91-1-4R	32	23	72.0
91-1-5R	48	34	70.8
91-1-7R	37	23	62.3
91-1-8R	40	23	57.6
91-1-11R	45	31	69.0
91-1-12R	23	12	52.2
91-1-13R	53	38	71.6
91-1-14R	22	16	72.8
91-1-15R	39	14	35.9
91-1-16R	24	16	67.7
91-1-19R	20	17	85.0
91-1-20R	39	24	61.5
91-1-23R	49	13	26.6
91-1-24R	33	18	54.6
Total	540	331	940.2
Average	36	22	62.6
74-1-4R	13	6	46.2
74-1-5R	73	29	39.8
74-1-8R	19	4	21.0
74-1-9R	51	13	25.5
74-1-11R	22	6	27.2
74-1-15R	41	11	26.8
74-1-[illegible]R	3	3	100.0
74-1-21R	19	8	42.2
74-1-22R	34	5	14.7
74-1-24R	23	8	34.8
74-1-25R	60	14	23.3
Total	358	107	401.5
Average	32.5	9.5	36.5
II-09-15-1-1R	28	20	10.7
II-09-15-1-3R	52	50	96.2
II-09-15-1-5R	21	21	100.0
II-09-15-1-6R	93	69	64.5
II-09-15-1-7R	38	38	100.0
II-09-15-1-8R	14	14	100.0
II-09-15-1-10R	18	13	72.2
Total	264	225	1069.7
Average	37.7	32.1	77.7

TABLE V

INDIVIDUAL PLANT SELECTIONS MADE IN 1919 FROM PARTLY WILTED PLANTS (PR), SELFED FOR TWO GENERATIONS IN THE GREENHOUSE, AND PLANTED ON SICK SOIL IN 1921

Selection	No. of plants	Wilted	
		No.	Per cent
M25-8PR	62	1	1.6
M25-9PR	24	5	20.0
M25-10PR	44	16	36.4
M25-11PR	20	20	100.0
M25-12PR	90	37	41.2
M25-14PR	34	17	50.0
Total	274	96	249.2
Average	45.7	16	41.5
25-7-28PR	20	1	5.0
25-7-29PR	16	3	18.8
Total	36	4	23.8
Average	18	2	11.9
175-1-26PR	13	2	15.4
175-1-27PR	71	10	14.1
Total	84	12	29.5
Average	42	6	14.8
91-1-26PR	24	12	50.0
74-1-26PR	9	0	0.0
74-1-27PR	34	9	26.5
74-1-28PR	53	20	37.8
74-1-29PR	14	6	42.9
Total	110	35	107.2
Average	27.5	8.8	26.8
II-09-15-1-14PR	57	57	100.0
II 09-15-1-19PR	101	96	95.0
II-09-15-1-21PR	31	30	96.8
Total	189	183	291.8
Average	63	61	97.3

TABLE VI

Summary of Results of Two Years' Selecting and Selfing

Selection	Parents	No. of individual plant selections		Total No. of plants produced		1920 Percentages			1921 Total percentage wilted	Total average for 1920 and 1921
		1920	1921	1920	1921	Wilted	Partly wilted	Total		
M25	R	5	3	186	131	17.8	42.4	62.0	38.3	50.2
	PR	11	6	612	274	17.4	41.1	61.5	41.7	51.6
	Average					17.6	42.7	61.8	40.0	50.9
25-7	R	43	20	1920	559	12.2	32.9	45.1	11.0	28.1
	PR	4	2	227	36	14.8	30.3	45.1	11.9	28.5
	Average					13.5	31.6	45.1	11.5	28.3
175-1	R	35	23	1284	1101	13.2	15.7	28.9	29.7	29.3
	PR	3	2	133	84	45.4	9.0	54.4	14.8	33.6
	Average					29.3	12.3	42.6	22.3	31.5
91-1	R	19	15	1302	540	11.0	41.4	52.4	62.6	57.5
	PR	1	1	103	24	7.7	37.0	44.7	50.0	47.4
	Average					9.4	39.2	48.6	56.3	52.5
74-1	R	17	11	1124	358	7.1	28.5	35.6	36.5	36.1
	PR	4	4	267	110	6.9	24.2	31.1	26.8	29.0
	Average					7.0	26.4	33.4	32.7	32.6
11-09-15-1	R	6	7	437	264	34.3	21.9	56.2	77.7	67.0
	PR	7	3	591	189	30.8	39.5	70.3	97.3	83.8
	Average					32.6	30.7	63.3	87.5	70.4

TABLE VII

COMPARISON OF PROGENY FROM WILTED (R) AND PARTLY WILTED (PR) FLAX PLANTS

Selection	Year	Parents		Deviation	D^1	$(D^1)^2$
		R	PR			
M25	1920	62.0	61.5	−0.5	1.63	2.65
	1921	38.3	41.7	+3.4	2.27	5.15
25-7	1920	45.1	45.1	0.0	1.13	1.28
	1921	11.0	11.9	+0.9	0.23	0.05
175-1	1920	28.9	54.4	+25.5	24.37	593.89
	1921	29.7	14.8	−14.9	16.03	256.96
91-1	1920	52.4	44.7	−7.7	8.83	77.97
	1921	62.6	50.0	−12.6	13.73	188.51
74-1	1920	35.6	31.1	−4.5	5.63	31.70
	1921	36.5	26.8	−9.7	10.83	117.29
II-09-15-1	1920	56.2	70.3	+14.1	12.97	168.22
	1921	77.7	97.3	+19.6	18.47	341.14
Totals				+13.6		1784.81

Mean deviation = 1.13. Standard deviation, 12.19.

$Z = \frac{1.13}{12.19} = 0.09$. When $Z = 0.1$ and the number of observations = 12, from Student's table it is found that $P = 0.6269$. From this the odds are found to be $\frac{0.6269}{1-0.6269}$ or 1.7 to 1 in favor of PR parents being more susceptible.

Odds of not less than 30 to 1 are regarded as significant.

TABLE VIII

COMPARISON OF PROGENY FROM R AND PR IN SELECTION FROM II-09-15-1 FOR 1920 AND 1921

Selection	Year	Parents		Odds
		R	PR	
II-09-15-1	1920	53.5	44.4	
	1920	52.0	57.8	
	1920	71.4	93.7	17 to 1 in favor
	1920	51.2	65.0	of PR parents
	1920	43.1	63.2	being more sus-
	1920	66.7	87.2	ceptible.
	1921	10.7	100.0	
	1921	96.2	95.0	

TABLE IX

CORRELATION TABLE FOR TOTAL PERCENTAGE OF WILT FOR INDIVIDUAL PLANT SELECTIONS FOR 1920 AND PERCENTAGE OF WILT FOR 1921

	5	15	25	35	45	55	65	75	85	95	
5	1	1	4	4	3	6	2				21
15		2	1	1	3	2		1			10
25	1	1	3	2	4	2			1		14
35	1	4	1	3	2						11
45	1	1	2	5		1					10
55	1		1		2		2				6
65				1	1		1	1	1	1	6
75				2		2	1				5
85						1		1			2
95					2	3	3		1	1	10
	5	9	12	18	17	17	9	3	3	2	95

Coefficient of correlation = 0.353 ± 0.066.

Table II includes the observations made on the number of plants produced from wilt-free parents in 1919, on the number and percentage killed by wilt, and the number and percentage partially wilted. The record of the number of plants killed outright was kept separate from that of the partially wilted plants in order to see if there was any tendency for resistant parent plants and partially resistant parent plants to produce partially wilted offspring.

Table III is similar to Table II except that it deals with the progeny from partially resistant instead of resistant plants.

It is apparent that, because of the comparatively small number of plants produced and the extremes of the variations, no reliable conclusions can be drawn as to the significance of the results recorded.

Elsewhere a further analysis of Tables II to VII is made in comparison with other results.

Table IV gives the results of the test with the progeny from resistant plants, after two years' selfing in the greenhouse, when tested on sick soil. The total number of plants is given, together with the number of plants wilted and the percentages of wilt.

Table V gives similar results from partially resistant parental plants in 1919.

The percentage of wilt for 1919 was not divided into wilted and partially wilted as in 1918. The percentage of wilted plants was noted, however, as in the preceding year. Notes on the percentages of wilt

were taken each week or ten days from the time of emergence to maturity. In 1921 any plants which were so badly wilted that they produced no seed were recorded under wilted. If all partially wilted plants had been included the percentage of total wilt would have been somewhat higher in 1921 than 1920, owing to the very high summer temperatures of 1921. The frequent counts necessitated considerable work but it was thought that the study of the progress of the disease would justify it. It was originally intended to analyze these data on the sequence of wilting, but there were so few that the analysis was not justified. The records from the 1921 tests indicate slightly more uniformity than do those from the 1920 tests. From these two tables alone few definite conclusions can be drawn.

From Table VI, which summarizes the data on individual plant selections for one and two years' selfing, several interesting conclusions may be drawn. There is little evidence of any correlation between "wilted" and "partly wilted" plants produced in the 1920 tests, or of any correlation with the fact of whether the parents had been resistant (R) or partly resistant plants (PR). Furthermore, an analysis of the entire table indicates that the progeny of "R" and "PR" parents were not essentially different. The only exception to this conclusion might be found in the selections from 11-09-15-1. In order to test this the results for the 1920 and 1921 tests were compared by Student's method and results are given in Table VII. There it is seen that the odds are much less than 30 to 1 for either the analysis of the progeny from all "R" and "PR" plants, or even for those from 11-09-15-1 alone, which are likewise analyzed in Table VIII. It is true that the analysis is not based on a uniform group of figures, but the figures are sufficiently large to make the conclusions fairly reliable. The explanation of the fact that resistant and partly resistant plants or that wilted and partly wilted plants can not be sharply delimited may be that *Fusarium lini* is only a facultative parasite the pathogenicity of which is influenced profoundly by environmental factors. Tisdale (21) has shown clearly how strongly soil temperature affects the development of the disease. Consequently, conditions seem to determine to a considerable extent the amount of injury which any particular plant suffers. It must be borne in mind that resistance to wilt in flax is only relative. The most resistant variety may wilt under severe conditions; while relatively susceptible strains may escape the disease in sick soil under certain favorable conditions. According to the figures in Tables VII and VIII the "R" and "PR" parental forms in any one group possessed approximately the same degree of resistance as was shown by their progeny. Each group seems to possess its own mean, and in comparing it with the mean of the parental form in the group

tests in Table XI, this mean has not been fundamentally changed by selections from wilt-resistant strains established by individual selection methods. Equally, there is no question that a new mean has been set for the selections made from M25 and from 11-09-15-1 in which more than 95 per cent wilting occurred uniformly before selection. Both these facts seem to be particularly significant in connection with a pure-line explanation of wilt-resistant varieties.

In Table VI is suggested the possibility of a correlation between the amounts of wilt resulting from these selections in 1920 and 1921.

Accordingly such a correlation table was made, Table IX. The coefficient of correlation was found to be $.353 \pm .066$. In view of the modifying factors that must be taken into consideration in comparing the wilt produced under field conditions in any one year with that of another year, this correlation appears to be quite significant. This brings out more forcibly perhaps than any other single analysis of these individual plant selection studies, the possible pure-line basis for interpreting the inheritance of wilt resistance.

A STUDY OF VARIATIONS WITHIN INDIVIDUAL SELECTIONS

Several individual selections made in 1919 were reselected in 1920. This was done within selections made in 1919 from non-selected varieties, M25 and 11-09-15-1. Each plant that produced seed in these selections was saved, classified, and labeled as wilt-free (R), or as partly wilted (PR). The seed from each plant was sown in a five-foot row in the plant pathology plots in the spring of 1921. In every case reselection seemed to be without effect. These plant rows, while varying considerably as might be expected in dealing with wilt resistance, were remarkably uniform as a series. Each series, however, differed markedly from the neighboring series, even when both were 1919 selections from the same variety. There undoubtedly would not have been such great uniformity if a larger number of 1919 selections had been taken for further analysis, as some of these probably would have proved to be heterozygous with segregation resulting. A most striking example of the uniformity of the reaction in the reselections is shown in Plate IV. On the left is the progeny of M25-14PR, which was obtained from eight plants, seven of which were marked "partly resistant," in 1920. On the right is shown the progeny from M25-5R, a most vigorous plant that stood out in sharp contrast to the rest of the susceptible plants when it was originally selected in 1919. Plate III shows this original selection. Seed was obtained from 43 plants which it produced in 1920. Each of these, 27 of which appeared to be wilt

free, were likewise planted in five-foot rows. The average percentage of wilt from these was 29.7, with the progeny from (R) and (PR) indistinguishable. The remarkable contrast between the progeny from M25-5R and M25-14PR is shown in Plate IV.

These studies seem to indicate at least two facts. (1) The original selection is the important one; subsequent selections, unless the plants are heterozygous, are of no avail in changing the resistance of the selection. There are different degrees of resistance in the original selection. M25-14PR produced some seed in 1920, and the selfed selection from the greenhouse produced seventeen plants in 1921 which, while not notably vigorous, produced some seed. Certain very susceptible varieties never produce plants that are able to grow beyond the very young seedling stage in sick soil. In accordance with Tisdale's (22) interpretation of resistance on the basis of multiple factors, it is probable that M25-14PR possesses only a part of them. (2) Resistance is not a character acquired by plants only after having been grown for several years on sick soil. Such selections as M25 appear vigorous and resistant as they occur scattered over the field the first year they are grown on sick soil. These retain their resistance in the immediate or successive progeny, and if they are "pure," as they appear to be in certain cases, resistance is not further built up and is not accumulative by an association of the host and the pathogene as has been commonly supposed to be the case.

LIMITS OF SELECTION

The preceding tests have indicated some of the limits of selection. It has been a rather common opinion that resistance could be developed in any variety by selection; Bolley thought (5, p. 179) (6, p. 181) that by growing an extremely susceptible variety on lightly infested soil, making selections there, and then transferring these successively to increasingly heavily infested soils, a high degree of resistance could be built up. This has not been thoroly tested in the experiments recorded here, but observations do not support this opinion. Seed of C. I. Nos. 186 and 190 grown at Mandan, North Dakota, were furnished by the United States Department of Agriculture. Several rows of these were planted in the plant pathology plots in 1919. One hundred per cent of the plants wilted within two weeks after emerging from the soil. There was absolutely no indication of resistance, quite in contrast to Minn. No. 25 which was grown as a susceptible check. The latter usually developed from 95 to 100 per cent wilt, with an occasional normal plant; and frequently several partly wilted plants which produced seed. The wilting usually occurred throughout the

season, a few plants being killed in the seedling stage and others following. This might be taken as an indication of a certain degree of resistance. There were no such indications in C. I. 186 and 190. However, the two latter were planted in a field in which so little wilt developed that Minn. No. 25 produced a fairly normal crop. Only a few plants of C. I. 186 and C. I. 190 survived. These were saved and seed was sown in sick soil in the plant pathology plots the following year. Again they did not get beyond the seedling stage. Three of the plants which survived from C. I. 186 were found later to be rogues which apparently resulted from a mechanical mixture of the seed. They were of a dwarf, much branched, almost procumbent type, highly resistant, but they in no way resembled C. I. 186.

These observations, in conjunction with the more detailed studies of individual selections such as were noted for M25-5R and M25-14PR, led the writer to conclude that resistance is either present in a variety or absent, and that if absent it can not be acquired gradually by the association of the plant with the fungus. It must be remembered in this connection that true resistance to a disease like flax wilt and disease-escaping qualities are not always easily distinguishable; but at least they should not be confused.

EFFECT OF CLEAN SOIL ON LOSS OF WILT RESISTANCE

Whether or not wilt-resistant varieties of flax are able to retain their resistance only when grown continuously in the presence of the disease-producing organism, is a most important question. It is of profound fundamental interest in relation to the nature of the inheritance of wilt resistance. It is obviously of much practical importance also. Bolley's (6, p. 177-78) studies of flax wilt led him to conclude that the growing of wilt-resistant varieties on non-infested soil resulted in the loss of the wilt-resistant qualities. In view of this it was advocated that a sick soil seed plot should be maintained. This peculiarity of disease resistance has been the subject of considerable discussion and interest among investigators. Jones, Walker, and Tisdale (15, p. 31), point out that in cabbage yellows, which is caused by *Fusarium conglutinans* Wollenw., it seems inevitable that in all the resistant strains there is a tendency to progressive reversion with a consequent loss of disease resistance which can only be met by continued selection from plants grown on sick soil. Their tests, however, with western seed produced on clean soil showed little or no loss of resistance.

In order to determine whether the growth of resistant varieties of flax on clean soil resulted in the loss of resistance, wilt-resistant selections which had been produced by both bulk and individual selection methods were grown on clean soil in isolated rows in corn plots on non-infested soil. Each year a part of the seed produced was saved for subsequent growth on clean soil and part was brought back to the plots to be compared with the corresponding selection which had been grown continuously on sick soil.

The results for two years' growth on clean soil are analyzed in Table X. This comparison is based on yields only. No appreciable difference is evident between the clean-soil series and the sick-soil series after two years' growth on clean soil. Consequently the analysis for 1920 was not made on the basis of wilt also. In one case the slight odds are actually in favor of the clean-soil series, the two latter are slightly in favor of the sick-soil series. However, neither of the differences may be considered as significant; for the odds, to be considered significant, should be thirty to one, while here they are in no case more than four to one.

TABLE X

Comparison of Results of 1920 Test for Loss of Wilt Resistance on Clean Soil for Two Years Computed by Student's Method

Selection	Clean soil Yield per acre, Bu.	Sick soil Yield per acre, Bu.	Odds	In favor of
Plot I–25 (Bulk selection)	5.35 8.00 4.10	7.78 14.90 6.02	3.8:1	Sick soil
Plot III–175–1	14.53 5.33 3.42	10.42 7.13 4.42	1.4:1	Clean soil
Plot IV–25–7	4.63 10.30 3.39	6.25 9.60 6.02	3.2:1	Sick soil

Table XI gives the results of the 1921 tests for the selections grown continuously on sick soil. Table XII gives the corresponding results for the same selections which had been grown on clean soil for three years (with the exceptions given in the footnote) and brought back for test on sick soil in 1921. Table XIII gives a comparison of Tables XI and XII on the basis of yield. The probable error was computed by the simplified "Minnesota method" (12). Table XIV gives a similar comparison on the basis of percentage wilted. The percentages of wilt were determined by careful counts made at regular intervals

throughout the growing season. Whether based on the amount of wilt or on yield, the differences are not significantly greater than the probable error of the differences except in the case of II-09-15-1, which is greater by a significant amount in both tables; and for Plot II 25-1, which on the basis of yield varies markedly in favor of clean soil because it was necessary to use 1918 seed for the sick-soil series. This seed germinated very poorly, producing only a few plants, as is shown in Table XII. On the basis of the percentage of wilt there is no evidence of a significant difference.

The marked differences in favor of sick soil in this one case (II-09-15-1) do not in reality indicate loss of wilt resistance due to growth on clean soil, but rather indicate the effect of bulk selection in producing resistance by growth on sick soil. In checking up the history of this selection which had been produced by the section of plant breeding for its desirable agronomic characters (see Table I), it was found that the first year of its growth on sick soil was at Crookston. There the soil on which it was grown in 1919 produced in reality little wilt—only 10 per cent in this variety. In the same season there was from 90 to 95 per cent wilt in the plant pathology plots at University Farm. Practically no seed was produced in 1919 on these plots. Consequently it was necessary to use Crookston seed for planting both series in 1920. It seems that the 1921 test, comparing the results from sick soil with those from clean soil, are really nothing more than a determination of the reduction in percentage of wilt by means of natural selection resulting from one year's growth on very sick soil when compared with its parental type. The inevitable conclusion is that wilt-resistant selections do not lose their resistance when grown on clean soil. This seems to be true regardless of the degree of resistance and of the method by which it was obtained. If the variety has not become uniform for resistance, natural selection merely stops and, in the case of a fairly close-fertilized crop, the proportion of resistant and susceptible plants does not change.

TABLE XI

Results of 1921 Tests for Effect of Clean Soil on Loss of Wilt Resistance—Sick-Soil Series in Which the Wilt-Resistant Selections Have Been Grown Continuously on Sick Soil

Selection	Row	No. of plants	No. wilted	Per cent wilted	Yield per acre, Bu.
	5	472	212	45	2.01
Plot I 25*	65	680	311	44	3.65
	116	492	132	27	5.23
Average	...	...	...	39	3.63
	11	293	103	35	1.51
Plot IV 25–7*	71	355	144	41	4.68
	122	358	59	16	4.72
Average	...	...	...	31	3.60
	17	663	88	12	9.83
Plot III 175–1†	77	353	83	15	11.45
	128	576	64	11	7.03
Average	...	...	...	13	9.44
	23	491	90	18	8.33
Plot II 91–1*	83	353	77	22	5.83
	134	375	66	18	4.58
Average	...	...	...	19	6.25
	29	413	159	39	4.68
Plot IV 74–1*	89	586	294	50	2.81
	140	512	164	32	3.34
Average	...	...	...	40	3.61
	35	590	242	41	2.97
Plott II-09-15-1‡	95	436	205	47	1.47
	146	471	238	50	2.09
Average	....	...	...	46	2.18
	41	121	50	41	1.91
Plot II 25–1*	101	60	28	47	0.60
	152	92	24	26	0.74
Average	....	...	...	38	1.08§
	47	297	166	56	2.83
Plot VI 25‖	107	559	320	57	0.81
	158	418	230	55	2.25
Average	....	...	...	56	1.96

* Grown on sick soil on plant pathology plots of University Farm continuously since 1914.

† Grown on sick soil on plant pathology plots of University Farm continuously since 1915.

‡ Grown at Crookston in 1919 on practically clean soil when there was only about 10 per cent of wilt in this variety. Grown on sick soil of the plant pathology plots, University Farm, in 1920 and 1921.

§ Grown from 1918 seed; germination very poor.

‖ Grown on practically clean soil at Crookston in 1919 and on sick soil in 1920 and 1921.

TABLE XII

RESULTS OF 1921 TESTS FOR EFFECT OF CLEAN SOIL ON LOSS OF WILT RESISTANCE—CLEAN-SOIL SERIES IN WHICH WILT-RESISTANT SELECTIONS HAVE BEEN GROWN FOR THREE YEARS, WITH EXCEPTIONS NOTED AWAY FROM SICK SOIL

Selection	Row	No. of plants	No. wilted	Per cent wilted	Yield per acre, Bu.
	8	562	242	41	2.71
Plot I 25	68	609	334	55	3.12
	119	583	135	23	5.27
Average	....	...	...	39	3.70
	14	688	331	41	2.80
Plot IV 25–7	74	675	345	51	3.55
	125	568	48	8	5.38
Average	....	...	...	33	3.91
	20	459	81	13	11.71
Plot III 175–1	80	388	50	11	9.40
	131	509	73	12	8.04
Average	....	...	...	12	9.72
	26	914	149	16	6.60
Plot II 91–1*	86	703	95	13	4.51
	137	402	135	34	4.15
Average	....	...	...	21	5.09
	32	711	211	30	4.29
Plot IV 74–1*	92	904	328	36	4.11
	143	617	261	42	2.50
Average	....	...	...	36	3.63
	38	1143	842	74	1.64
Plot II–09–15–1†	98	987	719	73	1.39
	149	554	516	93	0.29
Average	....	...	...	80	1.11
	44	845	328	39	6.33
Plot II 25–1	104	378	80	24	3.28
	155	338	133	39	4.60
Average	....	...	...	34	4.73
	50	889	504	57	3.33
Plot VI 25‡	110	657	442	67	1.56
	161	655	235	36	2.83
Average	....	...	...	53	2.57

* Grown on clean soil for one year, 1920, before being brought back onto sick soil of the plant pathology plots for comparison with the sick-soil series.

† A non-selected variety grown on practically clean soil at Crookston in 1919 and 1920.

‡ Non-selected Minn. No. 25 grown on clean soil continuously, so far as the records are obtainable.

All the other selections were grown on clean soil for three years, 1918, 1919, and 1920, before being brought back onto sick soil of the plant pathology plots for comparison with the sick-soil series.

TABLE XIII

SUMMARY OF DIFFERENCES IN MEANS OF YIELD WITH RESPECT TO EFFECT OF CLEAN SOIL ON LOSS OF WILT RESISTANCE

Selection	Average yield for series, Bu.		Differences in means, Bu.	Odds against occurrence of existing deviation*
	Clean soil	Sick soil		
Plot I 25..........	3.70 ± 0.47	3.63 ± 0.46	0.07 ± 0.7	Less than 1 to 1
Plot IV 25–7......	3.91 ± 0.49	3.60 ± 0.45	0.31 ± 0.7	Less than 1 to 1
Plot III 175–1.....	9.72 ± 1.24	9.44 ± 1.19	0.28 ± 1.7	Less than 1 to 1
Plot II 91–1.......	5.09 ± 0.64	6.25 ± 0.79	1.16 ± 1.0	About 1.3 to 1
Plot IV 74–1......	3.63 ± 0.46	3.61 ± 0.45	0.02 ± 0.6	Less than 1 to 1
Plot II–09–15–1....	1.11 ± 0.14	2.18 ± 0.27	1.07 ± 0.3	About 60 to 1
Plot II 25–1.......	4.73 ± 0.60	1.08 ± 0.14	3.65 ± 0.6	About 20,000 to 1
Plot VI 25........	2.57 ± 0.32	1.96 ± 0.25	0.61 ± 0.4	About 2.3 to 1

* Computed in accordance with "a table for estimating the probable significance of statistical constants," by Raymond Pearl and John Rice Miner, *In* Maine Agr. Exp. Sta. Bul. 226, pp. 85-88, March 1914.

TABLE XIV

SUMMARY OF DIFFERENCES IN MEANS OF WILT WITH RESPECT TO EFFECT OF CLEAN SOIL ON LOSS OF WILT RESISTANCE

Selection	Average per cent of wilt for series		Differences in means, per cent	Odds against occurrence of existing deviation
	Clean soil	Sick soil		
Plot I 25..........	39 ± 3.9	39 ± 3.9	0 ± 5.5	Less than 1 to 1
Plot IV 25–7......	33 ± 3.3	31 ± 3.1	2 ± 4.5	Less than 1 to 1
Plot III 175–1.....	12 ± 1.2	13 ± 1.3	1 ± 1.8	Less than 1 to 1
Plot II 91–1.......	21 ± 2.1	19 ± 1.9	2 ± 2.8	Less than 1 to 1
Plot IV 74–1......	36 ± 3.6	40 ± 4.0	4 ± 5.4	About 1 to 1
Plot II–09–15–1....	80 ± 8.0	46 ± 4.6	34 ± 9.2	About 8 to 1
Plot II 25–1.......	34 ± 3.4	38 ± 3.8	4 ± 5.1	About 1 to 1
Plot VI 25........	53 ± 5.3	56 ± 5.6	3 ± 7.7	Less than 1 to 1

EFFECT OF TIME OF PLANTING ON DEVELOPMENT OF FLAX WILT

Observations made on flax planted at various times seemed to indicate that the time of planting had considerable effect on the amount of wilt in both resistant and susceptible strains. In order to test this and to see what practical application it might have, particularly its effect on resistant varieties, time-of-planting tests were made in 1920 and in 1921. Results are given in Tables XV and XVI, and illustrated in Plates X to XIV inclusive.

These results show a marked relationship between wilt resistance and environmental conditions. Perhaps the erroneous impressions that have arisen regarding the nature of resistance in flax have been in part due to failure to appreciate this relationship. It will be noted from

Tables XV and XVI that the resistant varieties, when sown late, may be so severely affected by wilt that they produce practically no seed. On the other hand, a moderately susceptible variety like Minn. No. 25, when sown early, may so nearly escape the wilt that a fair crop is produced even on extremely sick soli.

The explanation of these results is undoubtedly to be found in the optimum temperature relations of the host and the parasite. Tisdale (21, 22) found that the optimum temperature range for the growth of the fungus was higher than that for the host. This, applied to field conditions, would mean that early-planted flax would grow more nearly under its most favorable conditions during the very early summer, and consequently be more vigorous and better able to withstand the infection. For later plantings this would not be true and, furthermore, the fungus would find its most favorable conditions of growth at the time when the host was not so vigorous. The practical significance of these results is apparent.

TABLE XV

Effect of Time of Planting on Development of Flax Wilt in Two Wilt-Resistant Selections. Planted on Sick Soil, University Farm, 1920

Selection	Date of planting	Per cent wilt	Yield per acre, Bu.
Plot IV 25–7	April 27	2	10.93
	May 7	5	8.48
	May 18	7	6.33
	May 30	50	0.46
Plot III 175–1	April 27	2	10.80
	May 7	5	7.77
	May 18	7	7.35
	May 30	40	2.38

TABLE XVI

Effect of Time of Planting on Development of Flax Wilt. Planted on Sick Soil, University Farm, 1921

Selection	Date of planting	Per cent wilt	Yield per acre, Bu.
Minn. 25 Non select	April 18	81	3.94
	May 1	84	1.54
	May 15	87	0.36
	June 1	94	0.36
Plot IV 25–7	April 18	28	10.25
	May 1	46	6.16
	May 15	53	1.16
	June 1	88	0.96
Plot III 175–1	April 18	11	9.79
	May 1	20	4.94
	May 15	12	4.89
	June 1	76	Undetermined

YIELD TESTS OF MINNESOTA WILT-RESISTANT SELECTIONS

The alarming decrease in flax acreage and in the production of linseed in this country which, as has been pointed out, is largely due to the presence of flax wilt, calls attention to the importance of finding some method of controlling the disease. Seed treatment, as was pointed out by Bolley (1, 2, 3), is important in lessening the amount of inoculum that may be carried to new lands. However, with the most careful seed treatment, this source of infection can not be entirely eliminated. Laboratory tests here have shown that the fungus can frequently be isolated from apparently sound seed that has been treated for five minutes with 1 to 1000 mercuric chloride. Furthermore, the available supply of clean land is decreasing each year. *Fusarium lini,* which is an accomplished saprophyte, persists for so long in the soil that crop rotation will not solve the problem satisfactorily. In 1920 observations were made at Crookston on a six-year crop rotation plot which included flax. The amount of wilt in one of these fields, which had grown one crop of flax six years previously, was striking when compared with the amount in the same variety on new land. Wilt was, of course, not nearly as serious as it would have been had flax followed flax, but the damage was considerable. Hope, therefore, centers primarily on the control of wilt by means of resistant varieties. Bolley demonstrated that this solution was practicable. Stakman et al. (20) confirmed Bolley's results and published the results of one year's tests of selections produced at the Minnesota station. Their results suggested that certain of these wilt-resistant selections yielded well. The criticism is sometimes made that resistant varieties do not yield as well on clean soil as do certain susceptible varieties. It is obvious that the ultimate test of the value of a variety is its ability to yield well.

The writer, through the courtesy of various co-operators, has been enabled to continue these experiments for four years. Table XVII gives the results of four years' tests on the extremely sick soil of the plant pathology plots. These yields were obtained from triplicated series of three rows each. The yields were computed from the central row of each series. Unfortunately, in 1919, the yields for Chippewa and Winona were based on a single determination. The last column gives the odds for comparison with Student's method which is used throughout in making comparisons for each table where it is applicable. Odds of thirty to one are considered significant.

Table XVIII gives the yields of the resistant selections and varieties on sick soil at Waseca for three years. Yields in this case were obtained from the central rows of triplicated three-row series.

Table XIX gives the results of similar tests for four years on sick soil at Mandan, North Dakota. These data were furnished by the Office of Cereal Investigations, United States Department of Agriculture. The yields were based on five-foot rows in triplicate.

It will be seen that in all the tests made in extremely sick soil, Winona and Chippewa yielded more, except at Waseca, where Chippewa did not yield quite so well. The odds in favor of Winona at University Farm and at Waseca are decidely significant.

Table XX gives the results of two years' tests on clean soil in the plant breeding nursery at University Farm. Yields are based on the central rows of triplicated three-row series.

Table XXI compares with Table XX, except that the tests are made on clean soil and the yields are based on triplicated seventeen-foot rows at Mandan. These data also were kindly furnished by the Office of Cereal Investigations.

Table XXII gives the results of two years' tests at Fargo, North Dakota, on land that had practically no wilt for these two years. These data were furnished through the kind co-operation of the North Dakota Agriculural College, and were based on triplicated rod rows.

Table XXIII gives the results of three years' tests at Crookston, Minn. These tests were made on soil that produced practically no wilt. Yields were obtained from the central row of each triplicated series of three rows, thirty feet long.

Table XXIV gives the results of one-fortieth acre field tests made by the agronomy department at University Farm. The soil was inoculated by the writer shortly after the plants had emerged, by growing the organism on sterilized wheat seed in large jars. After the organism had spread throughout the wheat, this was scattered over the field. The very susceptible varieties which were also grown developed much wilt, but not enough to make this a critical test of resistance comparable to those of the sick soil of the plant pathology plots. Hence in the summary table these results are grouped with the clean soil tests.

Table XXV gives the results of one-fortieth acre field tests on clean soil. These tests were made by the agronomy department and the data on yield were kindly furnished by them.

Table XXVI is a summary of the averages obtained from Tables XVII to XXV. From this it appears that the row tests gave much lower yields than did the one-fortieth acre plots. A comparison of these summary results is made by the Student's method in Table XXVII. Winona, Minn. No. 182 (175-1), appears to be pronouncedly superior to any other variety tested on sick soil. Chippewa, Minn. No. 181 (25-7), apparently yields as well as N. D. R. 114. On clean soil all three of these varieties yield about the same. Selection 91-1, Minn. No. 188, seems to yield exceptionally well on clean soil and averages practically as high as Chippewa or N. D. R. 114 on sick soil.

It was noted in the field that Chippewa was quite resistant to rust of flax caused by *Melampsora lini*.

TABLE XVII

Yield Tests of Selected Flax on Sick Soil, University Farm (Ten-Foot Rows)

Selection	1919		1920		1921		1922		4-yr. Av.		Odds
	Per cent wilt	Yield Bu.	Per cent wilt	Yield Bu.	Per cent wilt	Yield Bu.	Per cent wilt	Yield Bu.	Per cent wilt	Yield Bu.	
N. D. R. 114	29	2.65	48	6.01	32	5.06	20	3.84	32.30	4.39	Check
Chippewa (25–7)	4	8.66	11	9.02	31	3.60	10	3.22	14.00	6.13	9.80:1
Winona (175–1)	4.6	7.03	13	7.36	13	9.44	10	5.89	10.15	7.18	77.74:1
Plot 91–1	37	1.89	15	9.88	19	6.25	15	5.09	21.50	5.78	8.22:1
Plot 74–1	22	2.14	23	7.69	40	3.61	25	2.21	27.50	3.91	10.01:1
Plot II–09–15–1	91	0.00	55	3.02	46	2.18	30	3.16	43.60*	2.79*	

* Three-year average.

TABLE XVIII

Yield Tests of Selected Flax on Sick Soil, at Waseca (Thirty-Foot Rows)

Selection or variety	Yield per acre, Bu.				Odds
	1919	1920	1921	3-yr. av.	
N. D. R. 114	....	6.45	6.18	6.33*	......
Chippewa (25–7)	1.81	4.35	4.55	3.57	Check
Winona (175–1)	3.24	11.93	9.38	8.18	37.02:1
Plot II 91–1	2.61	7.86	1.18	4.15	3.57:1
Plot IV 74–1	0.90	2.70	0.95	1.52	33.22:1
Plot II–09–15–1	0.11	1.68	1.02	0.94	

* Two-year average.

TABLE XIX

Yield Tests of Selected Flax at Mandan, North Dakota, on Sick Soil (Five-Foot Rows)*

Selection or variety	Yield per acre, Bu.					Odds
	1919	1920	1921	1922	Average	
N. D. R. 114	2.6	4.3	1.9	12.0	5.2	Check
Chippewa (25–7)	1.0	5.3	2.4	15.8	6.1	4.31:1
Winona (175-1)	3.1	7.9	3.0	17.0	7.8	12.08:1
Plot II 91–1	1.2	3.0	2.4	10.2	4.2	17.21:1
Plot IV 74–1	1.7	2.7	2.5	15.1	5.5	1.53:1
Plot II–09–15–1	0.0	3.3	0.9	10.0	3.6	......

* These tests were made by the Office of Cereal Investigations, U. S. D. A., and the data were kindly furnished by them.

TABLE XX

YIELD TESTS OF SELECTED FLAX ON CLEAN SOIL AT UNIVERSITY FARM (SIXTEEN-FOOT ROWS)*

Selection or variety	Yield per acre, Bu.		
	1919	1920	Average
Chippewa (25–7)	2.44	9.60	6.02
Winona (175–1)	0.55	8.40	4.48
Plot II 91–1..........	5.58	10.79	8.19
Plot IV 74–1..........	2.80	9.10	5.95
Plot II–09–15–1	2.37	10.91	6.64

* Grown in plant breeding nursery.

TABLE XXI

YIELD TESTS OF SELECTED FLAX ON CLEAN SOIL AT MANDAN, NORTH DAKOTA

(ROD ROWS)*

Selection or variety	Yield per acre, Bu.				Odds
	1919	1920	1922	3-yr. av.	
N. D. R. 114......................	4.2	2.7	12.9	6.6	Check
Chippewa (25–7)	4.0	2.1	14.8	7.0	2.22:1
Winona (175–1)	5.5	2.7	14.2	7.5	1.34:1
Plot II 91–1......................	5.6	2.9	13.6	7.4	12.15:1
Plot IV 74–1......................	4.8	1.9	15.4	7.4	4.11:1
Plot II–09–15–1	2.6	2.0	13.0	5.9	

* These tests were made by the Office of Cereal Investigations, U. S. D. A., and the data were kindly furnished by them.

TABLE XXII

YIELD TESTS OF SELECTED FLAX ON PRACTICALLY CLEAN SOIL AT FARGO, NORTH DAKOTA (ROD ROWS)*

Selection or variety	Yield per acre, Bu.		
	1921	1922	Average
N. D. R. 114..........	9.2	15.3	12.3
Chippewa (25–7)	7.2	16.3	11.8
Winona (175–1)	8.1	16.0	12.1
Plot II 91–1...........	6.6	19.9	13.3
Plot IV 74–1...........	5.4	15.4	10.4

* These tests were made by the North Dakota Agricultural College. The data were furnished by them.

TABLE XXIII

YIELD TESTS OF SELECTED FLAX AT CROOKSTON ON COMPARATIVELY CLEAN SOIL (THIRTY-FOOT ROWS)

Selection or variety	Yield per acre, Bu.				Odds
	1919	1920	1921	Average	
N. D. R. 114	....	8.75	2.58	5.67	......
Chippewa (25–7)	14.92	5.02	2.16	7.37	4.74:1
Winona (175–1)	6.32	4.63	3.50	4.82	6.69:1
Plot II 91–1	13.60	6.51	3.58	7.90	3.23:1
Plot IV 72–1	14.41	7.65	2.72	8.26	Check
Plot II–09–15–1	5.25	8.17	2.19	5.20	3.98:1

TABLE XXIV

YIELD TESTS* OF SELECTED FLAX ON PARTIALLY SICK SOIL† AT UNIVERSITY FARM IN 1921 (ONE-FORTIETH ACRE PLOTS)

Selection or variety	Yield per acre, Bu.
N. D. R. 114	14.0
Chippewa (25–7)	13.4
Winona (175–1)	13.2
Plot II 91–1	16.8
Plot IV 74–1	11.6

* This test was made by the agronomy department, University Farm, and the data on yield were furnished by them.

† The soil was inoculated by the writer shortly after the plants emerged. Wilt developed quite heavily on White Blossom Dutch, an extremely susceptible variety, but was not heavy enough to give a reliable differential test.

TABLE XXV

YIELD TESTS OF SELECTED FLAX AT CROOKSTON, MINN., ON CLEAN SOIL (ONE-FORTIETH ACRE PLOTS)*

Selection or variety	Yield per acre, Bu.		
	1921	1922	Average
N. D. R. 114	7.06	13.91	10.49
Chippewa (25–7)	6.68	12.60	9.64
Winona (175–1)	8.09	14.57	11.33
Plot II 91–1	8.09	18.99	13.54
Plot IV 74–1	9.72	13.50	11.61

* These tests were made by the agronomy department, University Farm, and the data were furnished by them.

TABLE XXVI

SUMMARY OF AVERAGES FROM TABLES XVII TO XXV

Station	No. of years	Group	N.D.R. 114	Chippewa	Winona	91–1	74–1
		Sick soil					
University Farm	4	Row tests	4.39	6.13	7.18	5.78	3.91
Waseca	3	Do	6.33*	3.57*	8.18	4.15	1.52
Mandan	4	Do	5.20	6.10	7.80	4.20	5.50
Average	..	...	5.31	5.27	7.72	4.71	3.64
		Clean soil					
University Farm	2	Row tests	....	6.02	4.48	8.19	5.95
Mandan	3	Do	6.60	7.00	7.50	7.40	7.40
Fargo	2	Do	12.30	11.80	12.10	13.30	10.40
Crookston	3	Do	5.67	7.37	4.82	7.90	8.26
Average	..	...	8.19	8.05	7.23	9.20	8.00
		Clean soil					
University Farm	1	1/40 A. plot	14.00	13.40	13.20	16.80	11.60
Crookston	2	Do	10.49	9.64	11.33	13.54	11.61
Average	..	...	12.25	11.52	12.27	15.17	11.61

* Two-year averages.

TABLE XXVII

COMPARISON OF SUMMARIES OF YIELD TESTS FROM TABLE XXVI BY STUDENT'S METHOD

Selection	Tested on	Odds	In favor of
(N. D. R. 114) Check	Sick soil	Check	
Chippewa	Do	1:1	
Winona	Do	129:1	Winona
91–1	Do	3:1	N. D. R. 114
74–1	Do	4:1	N. D. R. 114
	Clean soil		
(N. D. R. 114) Check	(rows and plots)	Check	
Chippewa	Do	1:1	
Winona	Do	1:1	
91–1	Do	68:1	91–1
74–1	Do	1:1	

DISCUSSION AND CONCLUSIONS

Flax wilt undoubtedly has been one of the most important limiting factors in flax production in the United States. On account of the devastation caused by this disease, the center of flax production has continually moved westward. Flax should not be grown on the same soil more than once every ten or twelve years unless resistant varieties are available; in fact, it is questionable whether it can be grown that often. There seems to be evidence that the organism causing flax wilt may be present in most soils in those regions in which flax has ever been grown extensively. As *Fusarium lini* can live in the soil almost indefinitely as a saprophyte, and as it may persist within shriveled seeds or apparently sound seeds of flax, it is almost impossible to control it by ordinary methods of crop rotation or seed treatment. For this reason it has become necessary to attempt to develop resistant varieties.

Pioneer work on the control of flax wilt by means of resistant varieties was done by Broekema and by Bolley. Bolley demonstrated clearly that wilt-resistant strains could be obtained rather easily. He was inclined to think that resistance was developed in a variety as a result of constant association with the pathogene. In other words, a susceptible variety might be immunized artificially by association with *Fusarium lini*. This would be roughly comparable with artificial immunization in animals. But even in animals there is little or no evidence of such immunity being inherited. Presumably some toxin produced by the parasite promoted the production of anti-bodies in the host plant. Bolley was of the opinion that the degree of resistance was proportional to the length of time during which the strain or variety had been exposed to the disease. Furthermore, the permanence of the resistance would be roughly proportional to the length of time during which the immunizing process had operated. Practically, this meant that resistant strains could be developed in any variety of flax, but that several years might be required to produce these resistant strains. Naturally, resistant flax would lose its resistance if it was grown on clean land. The resistance of flax to wilt, then, would be quite different from the resistance to other plant pathogenes, because artificial immunity is practically unknown, if indeed it occurs at all in plants.

It is quite true that the wilt resistance of flax is only relative. Plants can be predisposed to attack and they can be protected against attack. The pathogene is greatly affected by temperature. Furthermore, the flax plant is rather sensitive to high temperatures, and therefore plants which normally are resistant under good growing conditions may be susceptible under poor growing conditions. The pronounced effect of soil temperature was shown first by Tisdale, and the writer has

demonstrated clearly that the amount of wilt which develops in either a resistant or a susceptible strain may be very greatly affected by soil temperatures. High soil temperatures are conducive to the development of a great deal of wilt because they are unfavorable to the flax plant and very favorable for the growth of the pathogene. The converse is true of low soil temperatures. When planted late in the season, when the soil temperatures are high, a resistant variety may be injured severely by wilt. On the other hand, a susceptible variety, sown early in the season when the soil temperatures are low, may produce a good crop. It is quite probable that the relative resistance of flax strains to wilt and the fact that the course of the disease is influenced so greatly by environmental conditions have obscured somewhat the true facts in connection with the production of wilt-resistant strains of flax.

All the results which the writer has obtained indicate rather clearly that wilt resistance is not built up by exposing plants to disease. It is thought that the resistant genotypes, if they may be called such, already exist in any variety in which there are resistant plants. When such varieties are sown on sick soil under temperature conditions favorable to the development of the disease, the non-resistant plants are eliminated and the resistant ones survive. Individual plant selection seems to be more efficacious than bulk selection simply because in practicing individual selection only the most resistant plants are saved. When bulk selections are made, however, the highly resistant and moderately resistant plants are saved as well as those which have merely escaped the disease on account of some fortuitous circumstances. The seed, therefore, consists of seed from resistant individuals, from moderately resistant ones, and from those which are susceptible but merely escape the disease. Naturally, when this seed is sown on sick soil, the resultant crop is not uniformly resistant. The evidence is perfectly clear that the selection of resistant flax strains consists merely in isolating genotypes which were resistant from the very beginning. Constant growing on sick soil, or on any other soil for that matter, does not change the genotypic composition of the plant with respect to wilt resistance. It would not be expected, therefore, that growing plants on clean soil would result in a loss of resistance. Experimental and observational evidence confirm this opinion.

Resistant varieties of flax which had been grown on clean soil for three years were just as resistant as strains of the same variety grown continuously on sick soil. It must be remembered, of course, that when a strain of flax is grown continuously on sick soil, the susceptible types are eliminated and only the most resistant remain. On the other hand, when a strain is grown on clean soil, the susceptible types are not

eliminated. It may appear, therefore, that a strain loses its resistance when grown on clean soil. As far as this carries any implication, however, that the germinal constitution of the strain with respect to wilt resistance is changed, the idea is erroneous. Resistance to *Fusarium lini* is an inheritable character comparable with any other genetic character.

In the course of the investigations, extensive observations were made on Chippewa, Minn. No. 181; and Winona, Minn. No. 182, both of which were selected originally by Stakman and Aamodt. The former was selected from Primost, Minn. No. 25, and is designated in the tables as 25-7, or as Plot IV 25-7; while Winona was selected from Blue Dutch, Minn. No. 175, and has been designated as selection 175-1, or as Plot III 175-1.

These varieties were compared with other resistant selections, under widely different conditions, on both clean and sick soil. On sick soil they showed a higher degree of resistance and greater yielding ability than any variety with which they were compared. The superiority of Winona was particularly marked. They also yielded well on clean soil when comparison was made with the best agronomic types. In addition to being highly resistant to wilt, Chippewa showed quite marked resistance to flax rust caused by *Melampsora lini*. One other selection has demonstrated good yielding ability. This is Selection 91-1, Minn. No. 188, which on clean land seems to out-yield anything with which it has been compared in these tests. On the extremely sick soil upon which the sick-soil yields are based, it averages almost as well as any of the resistant selections except Winona.

While it has been shown that the resistance to wilt is an ordinary genetic character inherent in certain genotypes within recognized flax varieties and that this character is not easily altered by environmental influences, it must be remembered that the reaction of both resistant and susceptible strains of flax is altered greatly by environmental influences. The difference is merely that between the genotypic and phenotypic phases.

The real nature of resistance is not yet known. Whether it is due to rapid growth, to morphological characters, or to a real physiologic incompatibility between the host and the pathogene must be determined by future investigations.

The possibility of the existence of elementary species or biologic forms of *Fusarium lini* also has been investigated by the writer, and, while preliminary results have been obtained, no final conclusions can be drawn at this time altho there is strong circumstantial evidence that there are different forms.

SUMMARY

1. Flax wilt, caused by *Fusarium lini,* has been shown clearly to be a limiting factor in the production of flax. On account of the fact that the pathogene is a soil saprophyte, it often is impossible to grow nonresistant varieties of flax on the same land profitably more than once every ten or twelve years. For this reason flax has been a migratory crop.

2. As *Fusarium lini* lives for a great many years in the soil and lives also in the seed, and as seed treatment is not entirely effective, the only practical method of controlling the disease is the use of resistant varieties.

3. Broekema first suggested the possibility of developing wilt resistant strains of flax. In the United States, Bolley developed several strains which are quite resistant to wilt.

4. The opinion has been prevalent that wilt resistance could be developed in susceptible varieties by association with the disease and that the permanence of this resistance was proportional to the length of time during which the strains had been grown in sick soil.

5. Experiments were made by the writer to obtain definite data on the mechanism by which resistant varieties are obtained, and to ascertain also the degree of permanence of this resistance and the degree to which it could be modified by environmental factors.

6. Individual plant selections were made from several varieties grown on sick soil. Seed was saved from the most resistant plants and from the partially wilted plants. When the progeny of these plants were selfed for two years, the degree of resistance was the same in all, with possibly one exception.

7. Apparently there are different degrees of resistance. Highly resistant plants can be obtained immediately by selection in the field. These plants bred true for resistance.

8. There are no indications that resistance is developed as a result of constant association with the pathogene. Resistant genotypes are present in certain varieties and obtaining resistant strains consists merely in selecting and propagating these genotypes.

9. Reselection or constant association with the disease does not change the degree of resistance of selected genotypes.

10. Not all varieties of flax contain resistant types. The development of resistant varieties, therefore, must be restricted to those varieties in which there are resistant genotypes.

11. The effect of growing flax plants on sick soil is merely to eliminate the susceptible strains and to permit the survival of resistant ones.

12. A wilt-resistant strain does not lose its resistance when grown on clean soil. The natural selection of resistant types, however, ceases to operate.

13. The optimum temperature for the growth of flax is fairly low, while that for the growth of the pathogene is relatively high. Consequently there will be more wilt when flax is grown at high soil temperatures than when it is grown at lower temperatures.

14. Wilt resistance is only relative, and the degree of resistance is therefore modified by environmental conditions.

15. Less wilt usually develops in flax sown early than in that sown later. Susceptible varieties can be grown successfully on sick soil provided the soil temperature is low; resistant varieties may be injured severely by wilt if the soil temperature is high.

16. Two superior wilt-resistant varieties have been developed at the Minnesota station. These are Chippewa, Minn. No. 181, a selection from Primost, Minn. No. 25; and Winona, Minn. No. 182, a selection from Blue Dutch, Minn. No. 175.

17. Extensive yield tests were made with Chippewa and Winona in comparison with other wilt-resistant selections. Winona consistently out-yielded most of the other resistant varieties.

18. Chippewa is not only resistant to wilt but also is moderately resistant to flax rust caused by *Melampsora lini*.

19. Selection 91-1, Minn. No. 188, produces well on sick soil, and yields exceptionally well on clean soil.

20. There is some evidence that there are several physiologic races of *Fusarium lini*, but this has not been demonstrated conclusively.

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PLATE I

Source of Individual Plant Selections Made in 1919

No. 175-1, a wilt-resistant individual plant selection made in 1916. Some of the tagged plants were the most vigorous, and others were partly wilted. The progenies of these were compared to determine the effect of continued selection.

PLATE II

Source of Individual Plant Selections Made in 1919

An unselected variety, No. II-09-15-1, grown on sick soil for the first time. Both vigorous and partly wilted plants were selected

PLATE III

Source of Individual Plant Selections Made in 1919

Minn. No. 25, M25-5R, the single plant shown in this picture, was the basis of selection. It was highly resistant in the first generation and was not modified by further selection.

PLATE IV

Effects of Reselection

The progenies of the plant illustrated in Plate III (M25-5R) and of a weak plant (M25-14PR) selected from the same variety (M25) at the same time were selfed in the greenhouse in 1919-20. The seed obtained was planted in 1920 and every plant was saved for testing on sick soil in 1921, as illustrated. The first four rows from the left in the two front series are the progeny of M25-14PR. The remaining rows to the right are the progeny of M25-5R. Reselection was without effect in either case.

PLATE V

Limitations of Selection

Selection C. I. 186 growing on clean soil. This selection was made by C. H. Clark for yield on clean soil at Mandan, North Dakota.

PLATE VI

Limitations of Selection

Selection C. I. 186 growing on sick soil. The only plant that was not killed by wilt proved to be the result of mechanical mixture in the seed. On less sick soil a few plants escaped. Some of them were saved. The progeny wilted as readily as the parent selection. A wilt-resistant selection in all probability could not be selected out of C. I. 186.

PLATE VII

Effect of Clean Soil on Loss of Wilt Resistance

The three rows on the right are selection Plot 1-25 on sick soil after three years' growth on clean soil. This was produced by bulk selection. The three rows on the left show the same selection that has been grown continuously on sick soil. Note that no loss of resistance appears from growth on clean soil. This was borne out by actual counts of wilted plants and by yield tests.

PLATE VIII

Effect of Clean Soil on Loss of Wilt Resistance

The three rows on the right are Selection 175-1 growing on sick soil after three years' growth on clean soil. The three rows on the left show the same selection grown continuously on sick soil. This selection was made in 1916 by the individual plant method. Note that there is no loss of resistance resulting from growth on clean soil, and further that selection has ceased to operate on sick soil. (See Plate IX.)

PLATE IX

Effect of Clean Soil on Loss of Wilt Resistance

The three rows on the right are Selection II-09-15-1 growing on sick soil after one year's growth on clean soil preceded by one year's growth on soil that was only partly sick. The three rows on the left show the same selection grown for two years on sick soil.

This apparent loss of resistance is not real, for the three rows on the right are as resistant as the selection was when it was put on clean soil. The three rows on the left from continuous growth on sick soil are better because growth in sick soil has resulted in natural selection.

PLATE X

Effect of Time of Planting on Development of Flax Wilt

The three rows on the left show Minn. No. 25, a moderately susceptible non-select variety, planted April 18. On sick soil. Compare with Plates XI, XII, XIII, and XIV.

PLATE XI

Effect of Time of Planting on Development of Flax Wilt

The three rows on the left show Minn. No. 25, a moderately susceptible non-select variety, planted May 1. On sick soil. Compare with Plates X, XII, XIII, and XIV.

PLATE XII

Effect of Time of Planting on Development of Flax Wilt

The three central rows show Minn. No. 25, a moderately susceptible non-select variety, planted May 15. On sick soil. Compare with Plates X, XI, XIII. and XIV.

PLATE XIII

Effect of Time of Planting on Development of Flax Wilt

The three rows on the left show Minn. No. 25, a moderately susceptible non-select variety, planted June 1. On the right is Plot IV 25-7, a highly resistant selection when planted early. On sick soil. Compare with Plates X, XI, XII, and XIV.

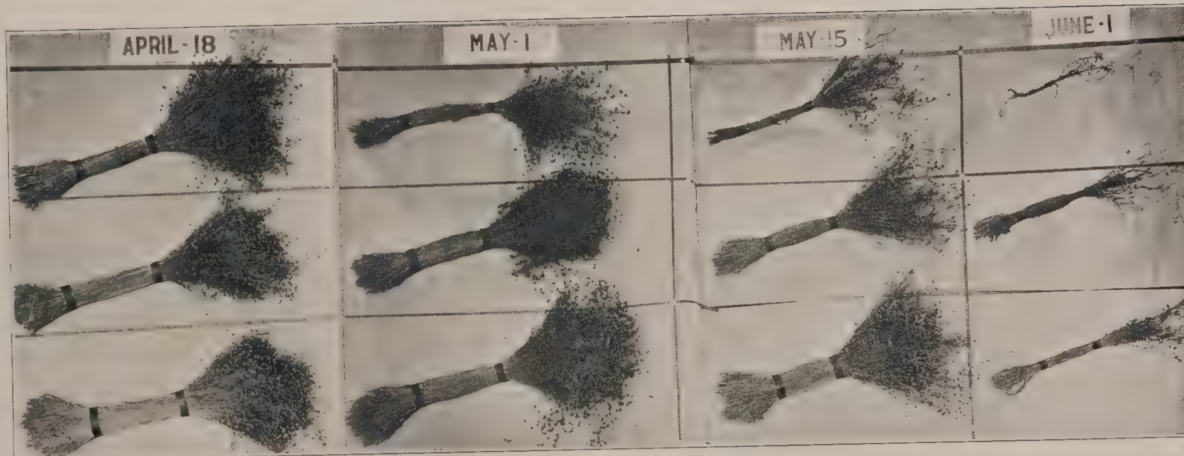

PLATE XIV

Effect of Time of Planting on Development of Flax Wilt

The upper row is Minn. No. 25, a moderately susceptible non-selected variety.

The central row is Chippewa (Selection Plot IV 25-7). This is a highly wilt-resistant variety of flax.

The lower row is Winona (Selection 175-1). This also is a highly wilt-resistant selection.

Note that with early planting a moderately susceptible variety may largely escape wilt, while a highly resistant selection is severely wilted if planted late when soil temperatures are high.

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